INTERSPECIFIC RELATIONSHIPS IN THE GENUS SETARIA

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Interspecific relationships in the genus *Setaria*

by

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1. Introduction

Setaria italica is cultivated widely under the common name of "Italian millet" in Eastern Asia, Middle East, Asia Minor, Russia, North America and Middle and Southern Europe. The wild *Setaria* species are distinguished from the cultivated species in certain characteristics regarding plant size, seed, panicle and bristle of panicle. The most significant difference is that the cultivated species does not shed the seeds at maturity, while the wild ones do.

De Candolle (1883), Koernicke (1885) and others reported about historical and ecological observations on *Setaria* species, and discussed the origin of the cultivated millet. Piper (1924), Stephens (1933), Rangaswami Ayyangar (1922), and others carried out the investigations on breeding of *S. italica*. The chromosome numbers of 19 species of *Setaria* are now known (cf. Darlington and Wylie 1955), and there is a polyploid series of 2x, 4x, 6x and 8x, the basic chromosome number being x=9.

As the flowers of *Setaria* species are small, emasculation and artificial crossing are not easy, but the present author found a new technique of emasculation and pollination, which has brought the crosses between *S. italica, S. viridis* and *S. Faberii* in success. Consequently the interspecific relationships between cultivated species, *S. italica,* and the wild species, such as *S. viridis* and *S. Faberii,* have been clarified.

The present paper deals chiefly with the interspecific relationships, based on the morphological, physiological and cytogenetic investigations. The studies have been conducted from 1938 through 1961 in Kyoto University, Japan.

2. Material and methods

Domestic species of *Setaria* were collected in Kyoto, Nishinomiya, Kobe, Kochi, Fukuoka and Kagoshima. While, some foreign species were collected by the present author herself in Montreal in Canada, and Braunschweig, Mannheim, Frankfurt a. M. and Darmstadt in Germany. Some species were supplied by the courtesies of a number of specialists, namely 51 varieties of *S. italica* from China, Hungary, Rumania, Bulgaria, Sweden, France, Poland, Finland, Germany, Holland and Czechoslovakia by Prof. Dr. HERMANN KUCKUCK, one variety of *S. italica* from Cape Town, in Africa, by Dr. RYOZO YOSHII, four varieties of *S. italica* from Kagoshima, *S. chondrachne, S. excurrens, S. autumnalis* OHWI and *S. verticillata* by Prof. Dr. YUZO MIYAJI, and one variety of *S. viridis* BEAUV. var. *pachystachys* MAKINO from Fukuoka by Dr. SHOZO NODA.

For the germination test an incubator was adjusted at 32° C, optimum after TAGUCHI (1947). The seeds were sown on moist filter paper in petri-dishes, or in sterillized soil in the greenhouse.

The root tips were kept first in cold distilled water (2°- 5° C) for 24 hours before the cytological fixation. Root tips were fixed in Carnoy's or Nawashin's solution, while flower buds exclusively in Carnoy's solution. PMC was observed by acetocarmine smear preparations, but paraffin sections, 12μ, were also used which were stained by Haematoxylin or Newton's gentian violet.

Some plants were grown in pots for the convenience of artificial cross pollination, which was carried out early in the morning under the fluorescence illumination. A day before the emasculation a panicle was cleared leaving 10 - 20 florets. The flowering of *S. italica* has two peaks daily at 6.00 - 7.00 in the morning and at 10.00 - 11.00 in the evening. The emasculation was difficult because the flower is very tiny and the stigma is entangled around the anthers. But the following method, which is more reliable than the bulk emasculation (MIYAJI, SASAKI and SHIN 1955 and CHANG 1958), has been found. Namely, i) as soon as the floret opens, the anthers come out without shedding pollen grains. The anthers are picked off carefully. ii) The anthers from the other parental floret are taken in the same way and are used for pollination.

For the preparation of the spodograms, 4 - 5 mm square excised from the middle portion along the midrib of the flag leaf was burnt in Werner's apparatus over weak flame for the first five hours and over strong flame for the following ten hours until the samples burnt out into white ash, and the ash sample was mounted in Canada-balsam.

3. Classification of *Setaria*

Morphologically and physiologically the species, domestic in Japan, have been classified into three groups as given in Tables 1 and 2.

Table 1.
Flowering season, size of stomata and pollen grains and fertility of *Setaria* species

Species	2n	Date of the first heading	Stomata	Pollen	Seed fertility
		Group 1			
Setaria italica					
nonglutinous	18	30/VI	31.8 μ	34.0 μ	89.0%
glutinous	18	30/VI	33.0	33.1	91.2
African	18	17/VII	33.3	32.7	88.8
S. viridis	18	23/V	32.8	32.9	87.8
S. viridis var. *pachystachys*	18	25/VI	32.5	32.9	82.0
S. pycnocoma	18	26/VII	33.6	33.7	26.0 93.1
S. Faberii	36	19/VI	45.7	45.7	81.3
S. verticillata	36	15/VI	35.9	37.3	87.7
		Group 2			
S. lutescens	36	6/IX	49.5	44.4	80.7
S. pallide-fusca	72	3/X	75.4	55.9	75.1
		Group 3			
S. chondrachne	36	4/X	43.5	4.9	30.0
S. excurrens	72	7/X	47.8	5.0	2.4

Table 2.
Characteristics of groups 1, 2 and 3 in the genus *Setaria*

Morphological character	Group 1	Group 2	Group 3
inflorescence	spike-like	spike-like	panicula
outer and inner glume surface	smooth	transversely rugose	smooth or transversely rugose
length of outer glume	same as the second empty glume	twice as long as the second empty glume	same or twice as long as the second empty glume
waxiness of panicle	nonwaxy	waxy	nonwaxy
colour of stigma	white	purple	white or purple
apical spikelet	fertile	sterile	fertile
flowering season	July - August	September - October	October - November
annual or perennial	annual with no rhizome	annual with no rhizome	perennial with rhizome

Group 1. i) The panicle is spike-like with green, brown or purplish brown bristles, arranged in two bundles (the first or lower bundle and the second or upper bundle). ii) The outer and inner glumes have a smooth surface and are as long as the second empty glume (Figure 1). iii) The stigma is white and the apical spikelet of the florescence bears one fertile floret, flowering from July to August. iv) The size of stomata and pollen grains are 31.8 - 45.7μ and 32.9 - 45.7μ respectively (Table 1).

S. italica (2x) is cultivated and there are glutinous and nonglutinous varieties in this species (Figure 2a).

S. viridis (2x) and *S. Faberii* (4x) resemble each other morphologically except that the plant size and seed size of *S. Faberii* are twice as large as the former (Figure 2 b,c). These two wild species appear morphologically to relate to *S. italica* closely.

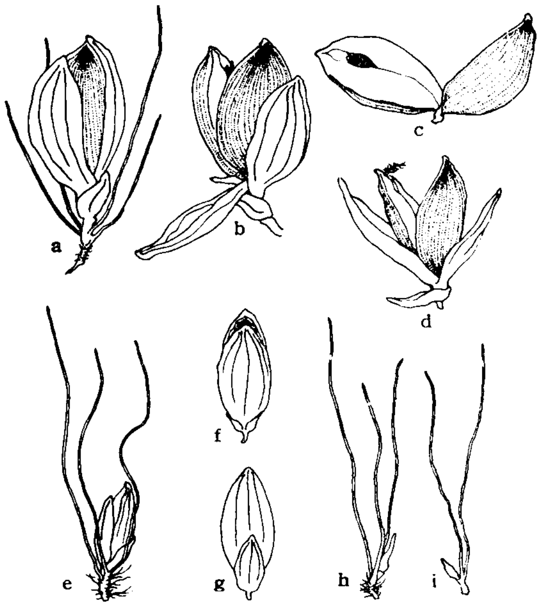
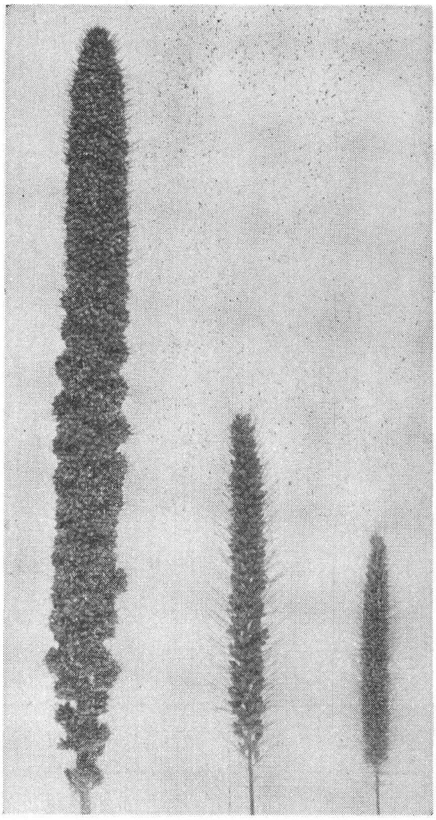


Fig. 1. Florets and bristles of *S. italica* (a-c) and *S. viridis* (d-i). Magnification × ca. 10

Table 3. The size of seeds of *Setaria* species

Species	2n	Seed length*	Seed width*
Setaria italica (L.) P. B.	18		
glutinous		1.48 mm	1.23 mm
nonglutinous		1.48	1.19
African		1.84	1.15
S. viridis Beauv.	18	1.45	0.63
S. viridis Beauv. var. *pachystachys* Makino	18	1.48	0.68
S. verticillata (L.) P. B.	36	1.29	0.69
S. pycnocoma (Steud.) Henr.	18	1.37-1.51	0.79-0.96
S. palmifolia (Koenig) O. Stapf	54	2.28	1.05
S. excurrens (Trin.) Miq.	72	2.22	0.93
S. chondrachne (Steud.) Honda	36	1.91	0.87
S. Faberii Herrm.	36	2.06	1.15
S. lutescens Hubbard	36	2.14	1.56
S. pallide-fusca Sch.	72	1.77	1.01

* Average value in 20 seeds



a b c

Fig. 2. Panicles of *Setaria* species of group 1.
a : *S. italica* nonglutinous, b : *S. Faberii*,
c : *S. viridis*

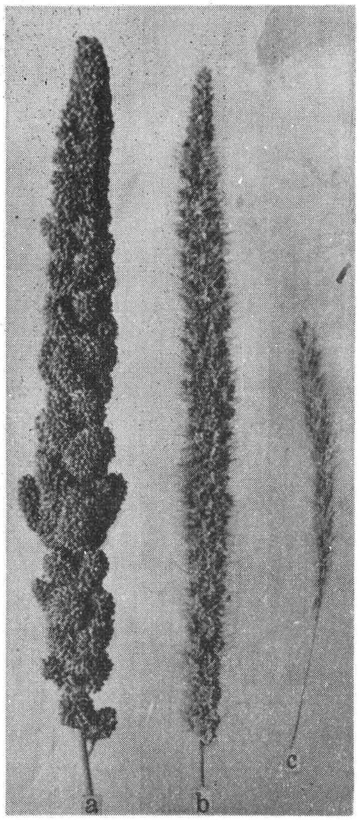
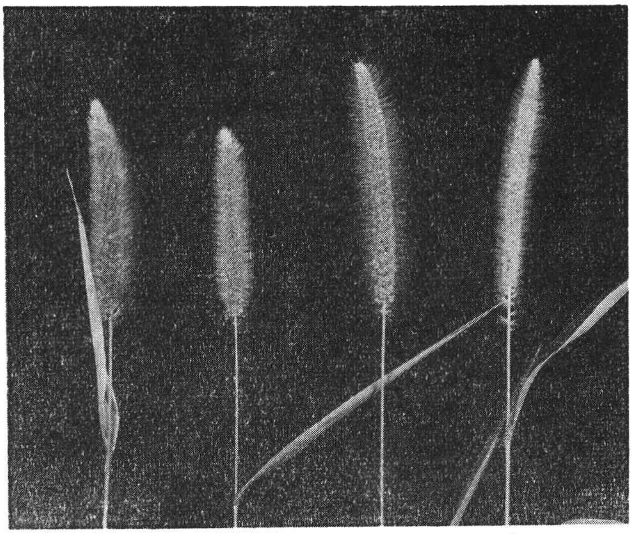


Fig. 3. Panicles of *S. italica* (a), *S. viridis* (c), and *S. pycnocoma* (b) (after Takenaka, Y.)

S. pycnocoma (2x) (Figure 4a-c) appears to be a natural hybrid between *S. italica* and *S. viridis*. According to a personal correspondence, Dr. Takenaka found the hybrid type in the fields of *S. italica* (Figure 3) during his visit to China. The frequency was 20 - 80% everywhere from Peiping to Hopeh. He observed in three successive generations, 1943-1945, morphological variations between *S. italica* and *S. viridis*, but neither typical *S. italica* nor typical *S. viridis* was found. According to the kind information of Dr. Miyaji, the present author observed the fields of *S. italica* in Kagoshima in November 1960, where the similar hybrid types were found. The hybrid types, varing in height between 50-130 cm, stood with erect panicles over the average *S. italica* with prostrate panicles. They were classified into following three types (Table 4). The 109 progeny individuals of these types were studied (Table 5).

(1) i) The *italica* type set yellow and elliptical seeds, with the germination ratio



a b c d

Figure 4. Panicles of *Setaria*, a-c: *S. Pycnocoma* and d: F_1 hybrid of *S, italica* (glutinous) × *S. viridis*

Table 4. Morphological and physiological characteristics of the seeds of *Setaria pycnocoma*

Type	Colour	Length × width	Germination	Leaf of seedling
italica type	yellow	spherical 1.48 × 1.24 sq/mm	83.30%	wide and long resembling *S. italica*
interm. type	light brown or brown	intermediate 1.51 × 0.91	22.82	intermediate
viridis type	dark brown	elliptical 1.36 × 0.80	1.43	narrow and short resembling *S. viridis*
S. italica	yellow	spherical 1.23 × 1.23	94.27	wide and long
S. viridis	dark brown	elliptical 1.45 × 0.63	0.54	narrow and short

Germination: in 2 months after harvesting

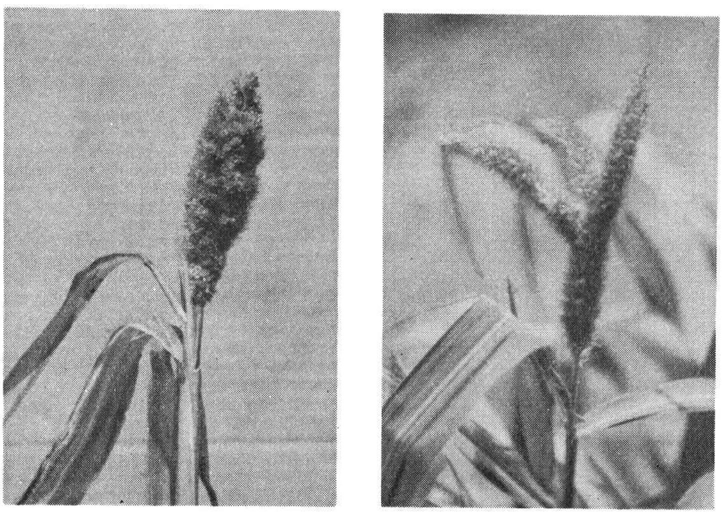
Table 5. Morphological and physiological characteristics of three types of *S. pycnocoma*

	Germination of seeds* (%)	Number of tillers						Leaf width (cm)	First heading
		1	2	3	4	5	6		
italica type	73.40 - 83.30	39	2	1	0	0	0	3.5-4.0	August
interm. type	40.83	38	3	0	0	0	0	2.5-3.5	late July to August
viridis type	6.78	3	10	7	3	2	1	2.5-3.0	early July

*: Germination test was made in 5 - 6 months after harvesting.

of 73.40 - 83.30 %, if sown soon after the harvest, indicating that they require no period of dormancy. ii) The first leaf of the seedling was wide and long like that of *S. italica*. iii) Among 42 individuals two had two tillers and others were non-tillering (Table 5). iv) The width of the leaf was 3.5 - 4 cm like that of *S. italica* and the time of the first heading was in August. v) Two nontillering individuals shot early in July and the panicles were short and compact with sporadical florets and a number of long bristles. Pollen fertility was ca. 27% (Figure 5a). Another individual with three tillers remained small (ca. 30 cm) and resembled *S. viridis*.

(2) i) The *viridis* type set dark brown and elliptical seeds, which are not different from those of *S. viridis* in appearance (Table 4). They germinated 1.43%, when sown within two months after the harvest (0.54 % in *S. viridis*) and 6.78 % when sown in five months after the harvest, indicating the requirement of certain period of dormancy. ii) The first leaf of the seedling was narrow and short like that of *S. viridis*. iii) Among 26 individuals three were nontillering and others had 2 - 6 tillers (Table 5). iv) The width of the leaf was 2.5 - 3 cm and the time of the first heading was early July. v) The plant height was 100 - 130 cm (Figure 6). In one strain, an individual of 30 cm was not different from *S. viridis* in appearance. vi) The pollen fertility varied from 28.12 to 84.25 %.



a b

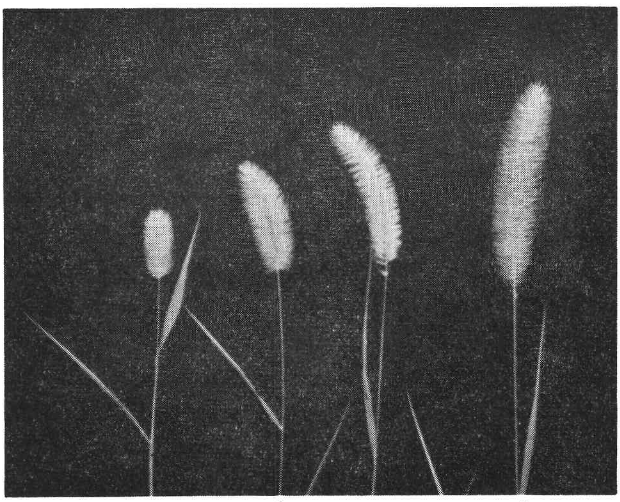
Figure 5. a : Panicle of *S. pycnocoma* from the seed of *italica* type, b: panicle of *S. pycnocoma* from the seed of intermediate type

(3) i) The intermediate type set brown seeds and they are not so elliptical as *S. viridis* and not so spherical as *S. italica* (Table 4). They germinated 22.82 % when sown soon after the harvest, and 43.11% when sown in five months after the

a b

Fig. 6. *S. pycnocoma* from the seeds of *viridis* type, a: the leaves are wide and many tillers are seen, b: a panicle.

harvest, indicating the requirement of certain period of dormancy. ii) The first leaf of the seedling was rather narrow but not short like that of *S. viridis*. iii) Among 41 individuals three had two tillers and others were nontillering. iv) The width of the leaf was 2.5 - 3.5 cm and the first heading was from late July to middle of



a b c d

Fig. 7. Panicles of a: *S. viridis* var. *pachystachys*, b: *S. viridis*, c: *S. verticillata* and d: *S. Faberii*

August. v) One nontillering individual bore a short and compact panicle but died before maturation. A panicle of another nontillering individual branched in three parts at the middle of the panicle (Figure 5b). Two nontillering remained small (25 - 30 cm). vi) The pollen fertility varied 26.01 % to 82.11 %.

S. viridis var. *pachystachys* grows only in the stony beaches under the warm and mild climate. Its panicle is ca. 3 cm long, and has soft and tufty bristles (Figure 7 a). The whole plant is only 20 cm in height, which is apparently adapted to the windy habitats. The seeds are similar in appearance to those of *S. viridis,* having a dark brown colour and small size (Table 3).

S. verticillata grows in subtropical regions (v. z. Okinawa, Formosa and the southern part of China) (Fig. 6c).

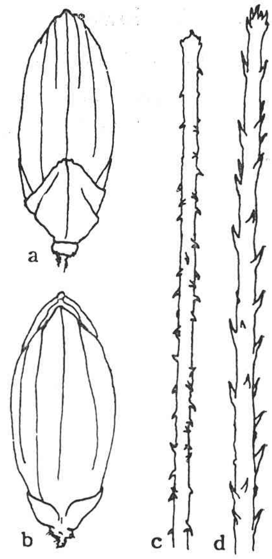


Figure 8. a-b: Matured florets with seed of *S. verticillata,* a : first and third empty glumes, b : second empty and outer glumes. c-d : Upper portions of bristles of c : *S. verticillata* and d : *S. Faberii* for comparison Magnification × ca. 19

The whole plant is green and the plant height is between *S. viridis* and *S. Faberii* (Figure 7 b, d), with rather erectpanicle, white stigma, dark brown and elliptical seeds, being the smallest in seed size among the author's collection (Table 3). The second empty glume is as long as the outer glume. The most significant characteristics of *S. verticillata* is the retrorse spinules of the bristle, while in all other species they are ascending (Figure 8). Owing to the retrorse spinules the panicles entangle each other when they come in touch by wind (Fig. 9).

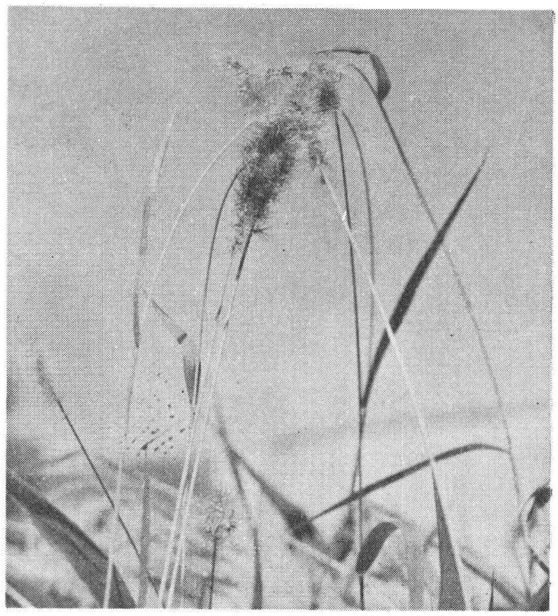


Figure 9. Panicles of *S. verticillata* entangled together by retrorse spinules of bristles

Group 2. i) The panicle is waxy and spike-like with yellowish-brown, reddish brown or reddish purple brisles, arranged in two bundles (the first or lower bundle and the second or upper bundle). ii) The outer and inner glumes have a transversely rugose surface and are twice as long as the second empty glume (Figure 10, 11). iii) The stigma is reddish purple and the apical spikelet is modified into bristles. The flowering season is September and October. iv) The size of stomata and pollen grains are 49.5 - 75.0μ and 44.4 - 55.9μ respectively (Table 3).

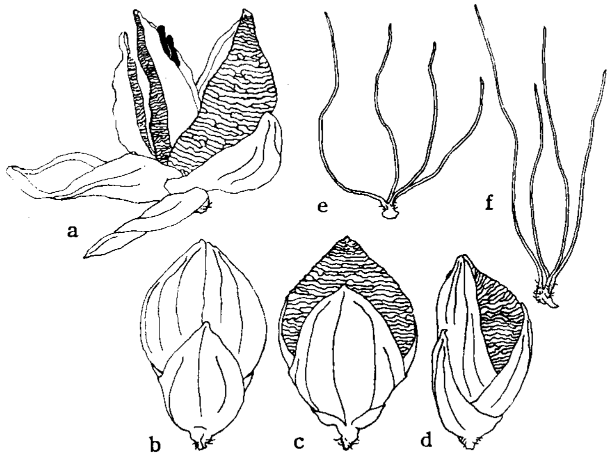


Figure 10. Florets and bristles of *S. lutescens* Magnification × ca. 10

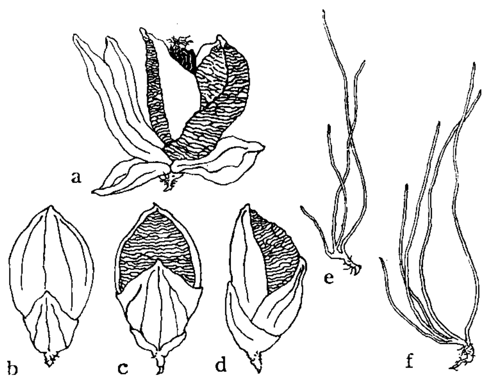
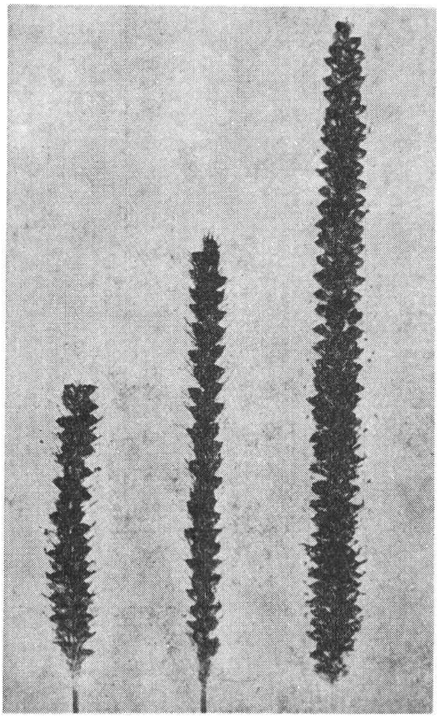


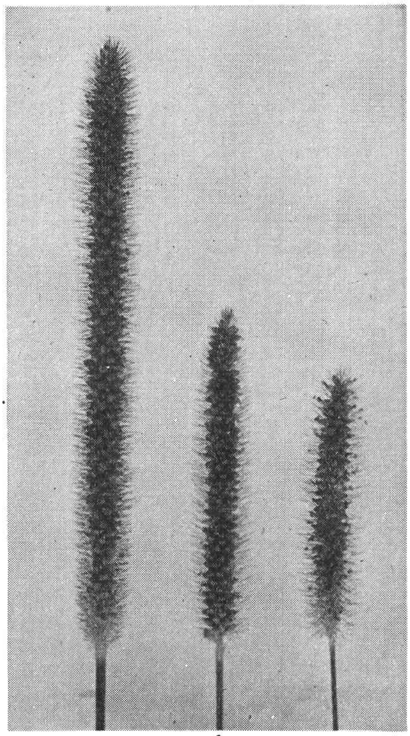
Figure 11. Florets and bristles of *S. pallide-fusca* Magnification × ca. 10

S. lutescens (4x) (Figure 12a) has an erect panicle with yellowish brown bristles which bears the largest seeds among the species of *Setaria* (Table 3). The waxy character is remarkably pronounced in this species and its panicle looks whitish, so that it is sometimes called *S. glauca*. The panicle length of a typical form is about 4 cm, but var. *longispica* has sometimes a panicle of about 14 cm (Fig. 12 b, c).



a b c

Figure 12. Variation in size in the panicles of *S. lutescens*



a b c

Figure 13. Variation in size in the Panicles of *S. pallide-fusca*

S. pallide-fusca (8x) (Figure 13 c) has a slightly prostrate panicle of 5 - 6 cm with reddish purple bristles which bears smaller seeds than *S. lutescens* (Table 3), while var. *longispica* has a panicle of 15 cm (Figure 13 a, b). Their flowering season started early in August. There are variations in bristle colour and seed size, some of which resembled *S. lutescens* very closely. The seed fertilities of those variations were ca. 80%.

Group 3. i) The panicle has panicula inflorescence (Figure 14), while the panicles of groups 1 and 2 are spike-like. ii) All three species of this group are perennial, while those of groups 1 and 2 are annual. iii) The inner and outer glumes have a smooth surface in *S. chondrachne* and transversely rugose surface in *S. palmifolia* and *S. excurrens* (Figure 15). iv) The size of stomata of *S. chondrachne* and *S. excurrens* are 43.5μ and 47.8 μ (Table 3). v) The flowering season is October.

S. chondrachne (4x) is found in the western and southern part of Japan.

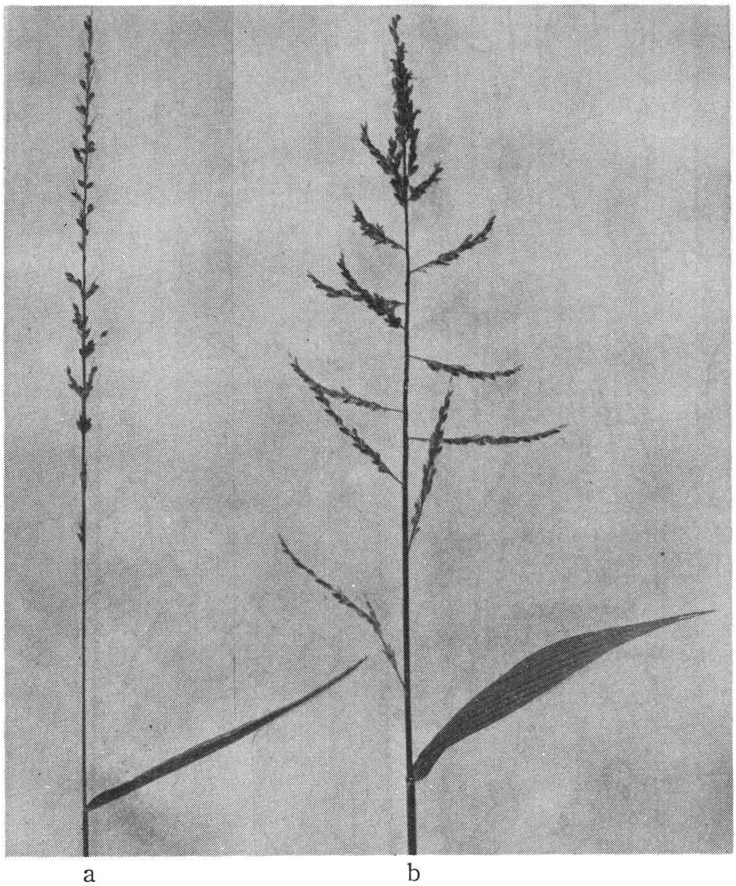
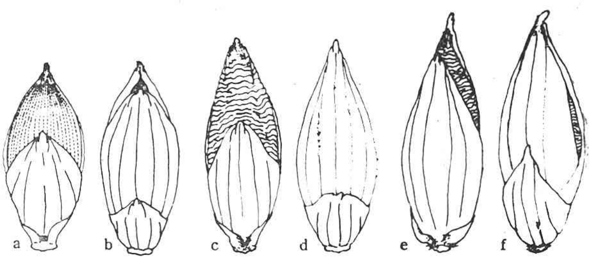


Figure 14. Panicles of *S. chondrachne* (a) and *S. excurrens* (b)

Fig. 15. Matured florets with seeds of *S. chondrachne, S. excurrens* and *S. palmifolia*, showing the surface of inner glume, outer glume and empty glumes, a, b: *S. chondrachne*, c, d: *S. excurrens*, e, f: *S. palmifolia* Magnification ca. $\times 12$



S. palmifolia (6x) and *S. excurrens* (8x) occur in Kyushu in Japan.

It is observed that the stigma of *S. chondrachne* and that of *S. excurrens* were purplish red. The flower of *S. palmifolia* has not been observed yet.

Setaria from foreign countries

S. viridis from Montreal, Braunschweig, Mannheim, Darmstadt and Frankfurt a.M. germinated contemporaneously with the domestic one. The Montreal and Braunschweig *viridis* grew 10 - 20 cm tall, bore small panicles of about 3 cm in length, and flowered 2 - 3 weeks earlier than the domestic one. Their fertilities were 46.27% and 35.71% respectively. The Mannheim and Darmstadt *viridis* grew only about 5 cm tall, and bore small and poor panicles, which flowered 3 - 4 weeks earlier than the domestic *viridis* (Figure 16 b) and six seeds from the Darmstadt *viridis* have been obtained (Table 6).

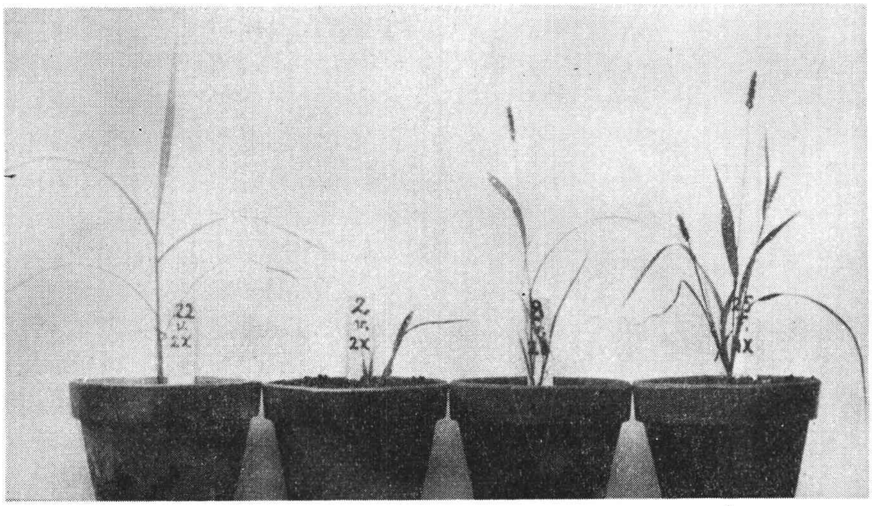
Table 6. *Setaria* species collected from foreign countries

Species	Locality	2n	The first * heading	Stomata size	Fertility **	Plant height
S. viridis	Montreal	18	9/VI	31 .3 μ	46 .27 %	25 cm
S. viridis	Braunschweig	18	6/VI	30 .4	35 .71	30
S. viridis	Mannheim	18	7/VI	30 .2	2 seeds***	5
S. viridis	Darmstadt	18	7/VI	30 .9	6 seeds***	5
S. Faberii	Montreal	36	11/VI	35 .0	85 .72	50
S. lutescens	Mannheim	36	30/VII	63 .0	78 .32	40
S. lutescens	Frankfurt a.M.	36	2/VIII	58 .2	76 .73	50

* Sown 3/V; ** fertility in Kyoto; *** a few seeds were found in about ten panicles.

S. Faberii from Montreal grew normally in size but their first heading was seen early (June 18). The seed fertility was 85.72% (Table 6).

S. lutescens from Mannheim and Frankfurt a. M. grew normally in size, but their first heading was about four weeks earlier than the domestic one. Their fertilities were 79.32% and 76.73% respectively (Table 6).

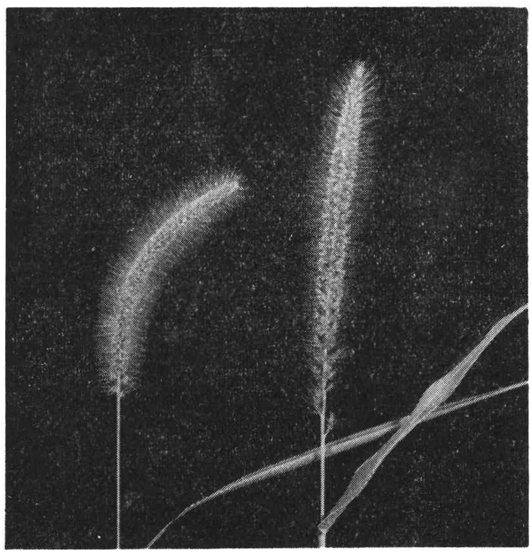


a b c d

Figure 16. *S. viridis* from foreign countries, a : *S. viridis* from Kyoto, Japan, b : *S. viridis* from Mannheim. Germany, c : *S. viridis* from Montreal, Canada, d : *S. Faberii* from Montreal (photo June 14, 1960)

S. italica from Africa is non-glutinous and has several wild characteristics, v. z. 6 - 9 tillers, long and abundant bristles, elliptical and reddish orange coloured seeds and narrow leaves (3.5 cm). However, the seeds does not shed at maturation and the plant height is ca. 100 centimeter (Figure 17 b).

S. italica from China and several countries in Europe were all non-glutinous and germinated 80 - 97%. Variations were observed in seed colour and form. Two strains from France died at the seedling stage when they were sown in the middle of July and late July. Probably they are not adapted to the temperature of 31° - 35° C.



a b

Figure 17. Panicles of F_1 hybrid of *S. italica* (African) × *S. viridis* (a) and *S. italica* (African) (b)

4. Germination and dormancy of seeds

The 1937 seeds of *S. italica, S. viridis, S. Faberii, S. lutescens* and *S, pallide-fusca* were tested for germination for five years until 1942. They were kept in paper bags in a wooden chest of drawers in the laboratory and sown every year in May. In the first year they showed a germination percentage of 80 - 90%, but in the second year the percentage dropped to 10 - 20%. In the third and fourth year the percentage of wild species did not drop so much, but that of the *S. italica* dropped to 2 - 5% *S. lutescens* showed the lowest percentage and *S. Faberii* the second lowest among the wild ones. In the fifth year *S. italica, S. Faberii, S. lutescens* and *S. pallide-fusca* did not germinate at all, while *S. viridis* germinated about 0.2%. Based on these experimental data it has been known that the germination ability of the seeds of *Setaria* is nearly or entirely lost in about five years.

The seeds of any variety of *S. italica,* germinated in the incubator (30° - 32° C) with high percentages (over 93) in about two months after harvest. Among the wild species, *S. chondrachne* and *S. verticillata* gave 97.0% and 40.0% respectively. Accordingly, these three can be said to have no dormancy period. The seeds of *S. viridis, S. Faberii, S. lutescens, S. pallide-fusca* and *S. excurrens* were found to require a certain dormancy period.

Italica type of *S. pycnocoma* showed the germination percentage of 73.03%, *viridis* type 1.43% and intermediate type 22.82%. Based on these data the intermediate type and the *viridis* type seem to require a certain dormancy period.

The duration of the dormancy period: the seeds were sown in soil in a greenhouse without heating, 20 - 30 days after the harvest. The dates of sowing were September 27, 1960 for group 1 and November 20 - December 19, 1960 for group 2. *S. italica* and *S. viridis* started to germinate around February 15, 1961 and the germination was completed by March 10 - 13. 1961.

It is interesting to note that the dates of germination of all the domestic species are approximately the same. The seeds of *S. Faberii* and *S. lutescens* from Canada and Germany germinated in the beginning of March, 1961.

In order to test, whether the low temperature affects the duration of the dormancy period, the 1960 seeds of *S. viridis, S. Faberii, S. lutescens* and *S. pallide-fusca* were kept in a moistened vinyl bag in the refrigerator regulated at 2° - 5° C. Some of the seeds of each species were taken out of the refrigerator one month later and tested for germination in an incubator (30° - 32° C). The rest of the seeds were tested in the same way two months later. But no seeds germinated in either of these experiments. The low temperature treatment of 1 - 2 months was not effective to break the dormancy.

5. Seasonal analyses of wild population

The species which occur spontaneously in the districts of Kyoto, Osaka and Kobe are mostly *S. viridis* and *S. Faberii* of group 1 and *S. lutescens* and *S. pallide-fusca* of group 2. The observation has been made on these species in the experimental field of the University of Kyoto as well as in nature around the campus and in the vicinities of Kyoto, Kobe and Nishinomiya.

The species in group 1 started to flower late in June and reached the height of flowering in July to August. In September, the flowering became sporadically. Some plants continued branching and flowering, but the floret did not open completely or if it did, anthers dehisced incompletely.

The species of group 2 generally began to flower toward the end of August. One strain of *S. pallide-fusca* started flowering early in August. But in other strains of *S. pallide-fusca* and in *S. lutescens* flowered during September and October, and they continued flowering until the first frost in November. In the later season the flowering became irregular and anthers did not dehisce completely. Such difference in flowering seasons between groups 1 and 2 hinders their natural hybridization.

For the observation of seasonal succession of *Setaria* species, 24 representative plots of 1 - 10 square meters were selected in the campus of the Kyoto University and around the author's residence in Nishinomiya (Table 8).

i) In 13 plots (Nos. 1, 3, 4, 5, 6, 8, 9, 11 - 16) the species of group 1, *S. viridis* and *S. Faberii,* were commonly found.

ii) In four plots (Nos. 19, 20, 21, 23) the species of group 2, *S. lutescens* and *S. pallide-fusca,* were growing.

iii) In two plots (Nos. 15, 24) *S. viridis, S. Faberii* and *S. pallide-fusca* were growing mixed in about equal number.

iv) In plot No. 22 *S. Faberii,* in plot No. 10 *S. viridis* and in plot No. 9 *S. viridis* and *S. Faberii* were growing sparsely mixed among the species of group 2.

In general simple populations of *S. viridis* were observed more frequently than those of *S. Faberii.* The low fertility was used as a clue of finding the hybrid if it occurred in the mixed population of *S. Faberii* and *S. viridis.* But actually no plants with a low fertility were found, indicating that there is very little chance of hybridization between the two species. The artificial crosses in the combination of *S. viridis* (♀) × *S. Faberii* (♂) gave less seeds than in the reciprocal combination (Table 8). Only one of 14 seeds of *S. Faberii* (♀) × *S. viridis* (♂) germinated.

S. lutescens (4x) and *S. pallide-fusca* (8x) often grow mixed together. The plant height of these two species is similar (30 - 50 cm) and their flowering seasons are close to each other or same. Hwoever, since three seeds of *S. lutescens* × *S. pallide-*

Table 7. Seasonal succession of *Setaria* species

Habitat	Plot No.	Period of observation	Number of panicles observed				Area
			Group 1		Group 2		
			vir.	*Fab.*	*lut.*	*pall.*	m × m
Kyoto Univ.	1	28/VII-18/IX	16	13	-	-	(2 × 1)
	2	28/VII-22/IX	21	-	-	-	(3 × 1)
	3	28/VII-25/IX	33	42	-	-	(2 × 1)
	4	5/VIII-20/IX	92	7	-	-	(3 × 2)
	5	3/VIII-10/IX	13	52	-	-	(3 × 5)
	6	3/VIII-10/IX	21	13	-	-	(4 × 1.5)
	7	3/VIII-10/IX	30	-	-	-	(6 × 1)
	8	3/VIII-12/IX	23	46	-	-	(4 × 2)
	9	3/VIII-10/IX	12	15	-	48 purple	(3 × 1)
	10	3/VIII-10/IX	12	-	-	87 purple	(4 × 5)
	11	20/VII-10/IX	522	360	-	-	(2 × 3)
	12	20/VII-10/IX	40	190	.	-	(3 × 2)
	13	8/VIII-10/IX	17	200	-	-	(0.5 × 3)
	14	9/VIII-10/IX	49	12	-	24 br. purple	(2 × 1)
	15	9/VIII-10/IX	50	19	-	60 purple	(1 × 1)
	16	9/VIII-18/IX	55	44	-	-	(1 × 1)
Nishino-miya	17	15/VIII-30/IX	63	-	-	-	(1 × 2)
	18	31/VIII-10/X	-	35	-	-	(10 × 1)
	19	31/VIII-10/X	-	-	-	56 red. purple 11 br. purple	(2 × 1)
	20	31/VIII-10/X	-	-	-	213 red. purple 5 br. purple (*longispica*)	(1 × 3)
	21	31/VIII-10/X	-	-	15	20 yel. purple	(1 × 1)
	22	31/VIII-10/X	-	18	12	320 purple 11 red. purple	(5 × 1)
	23	31/VIII-10/X	-	-	32	-	(1 × 1)
	24	31/VIII- 9/X	-	52	-	60 yel. purple 8 red. purple	(1 × 3)

fusca and five seeds of *S. pallide-fusca* × *S. lutescens* did not germinate, it is thought that the hybridization between the two species occur very seldom, in other words they are isolated physiologically.

Table 8. The result of crosses among five species of *Setaria*

♀ \ ♂		*ital.* U	*ital.* M	*ital.* A	*vir.* (2x)	*vir.* Mont.	*Fab.* (4x)	*lut.* (4x)	*lut.* Fr.	*pall.* (8x)
ital.	U		19 10 5	-	48 38 8	-	5 0 0	-	-	-
	M	35 28 16		-	24 16 6	26 18 15	39 7 0	-	-	-
	A	6 5 5	-		3 2 2	-	-	-	-	-
vir.		26 14 8	38 10 8	-		1 0 0	69 10 0	-	-	-
	Mont.	-	6 0 0	-	6 5 0		-	-	-	-
Fab.		14 2 0	12 5 0	-	67 14 1	-		4 0 0	-	-
lut.		-	-	-	-	-	3 0 0		-	6 3 0
	Fr.	-	-	-	-	-	7 0 0	-		-
pall.		-	-	-	-	-	-	23 5 0	-	

ital.: *italica,* U: nonglutinous, M: glutinous, Fab.: *Faberii,* A: African, vir.: *viridis,* Mont.: *viridis* from Montreal, lut.: *lutescens,* Fr.: *lutescens* from Frankfurt a. M., pall.: *pallide-fusca.* The three figures in each quadrangle, from top to bottom, indicate number of pollinated florets, number of hybrid seeds and number of plants obtained, respectively.

6. Comparative morphology of epidermal structures

Sump preparation

i) *S. viridis* (2x), *S. viridis* var. *pachystachys* (2x), *S. Faberii* (4x) and *S. verticillata* (4x) have many spinules and stripes of narrow veins at approximately equal distances. The cells of the diploid species are smaller than those of the tetraploid species (Table 1. Figure 18).

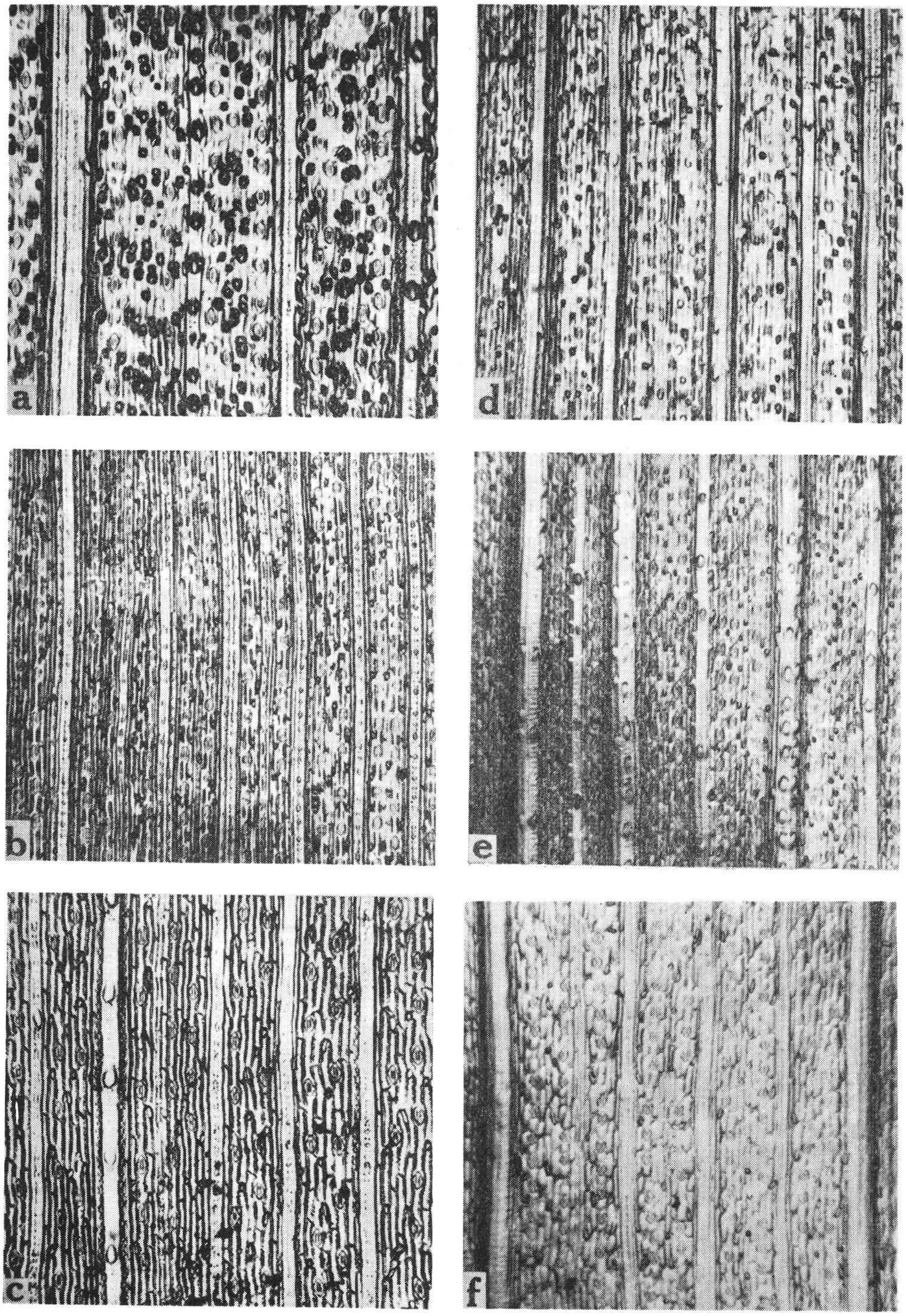


Figure 18. Sump patterns of under surface of leaves of *Setaria* species, a: *S. italica*, b: *S. viridis*, c: *S. Faberii*, d: *S. viridis* var. *pachystachys*, e: *S. pycnocoma*, f: *S. verticillata* Magnification × ca. 80

ii) *S. italica* (2x) has stripes in various width at irregular distances and abundant spinules on veins and among the other cells between the veins. The spinules press the cell walls aside and make them irregularly (Figure 18).

iii) *S. pycnocoma* (2x) shows many spinules on veins like *S. italica* but the spinules between veins are small like *S. viridis* and less in number than *S. italica* so that the cell walls are not pressed aside (Figure 18).

iv) *S. lutescens* (4x) and *S. pallide-fusca* (8x), have spinules very few and the stripes of veins are not remarkable. The cells of the tetraploid species are smaller than those of the octoploid species (Table 1, Figure 19).

v) The F_1 hybrid of *S. italica* × *S. viridis* has stripes at approximately equal distance like *S. viridis*, and abundant spinules on veins and among the other cells like *S. italica*, making the cell walls irregularly (Figure 19).

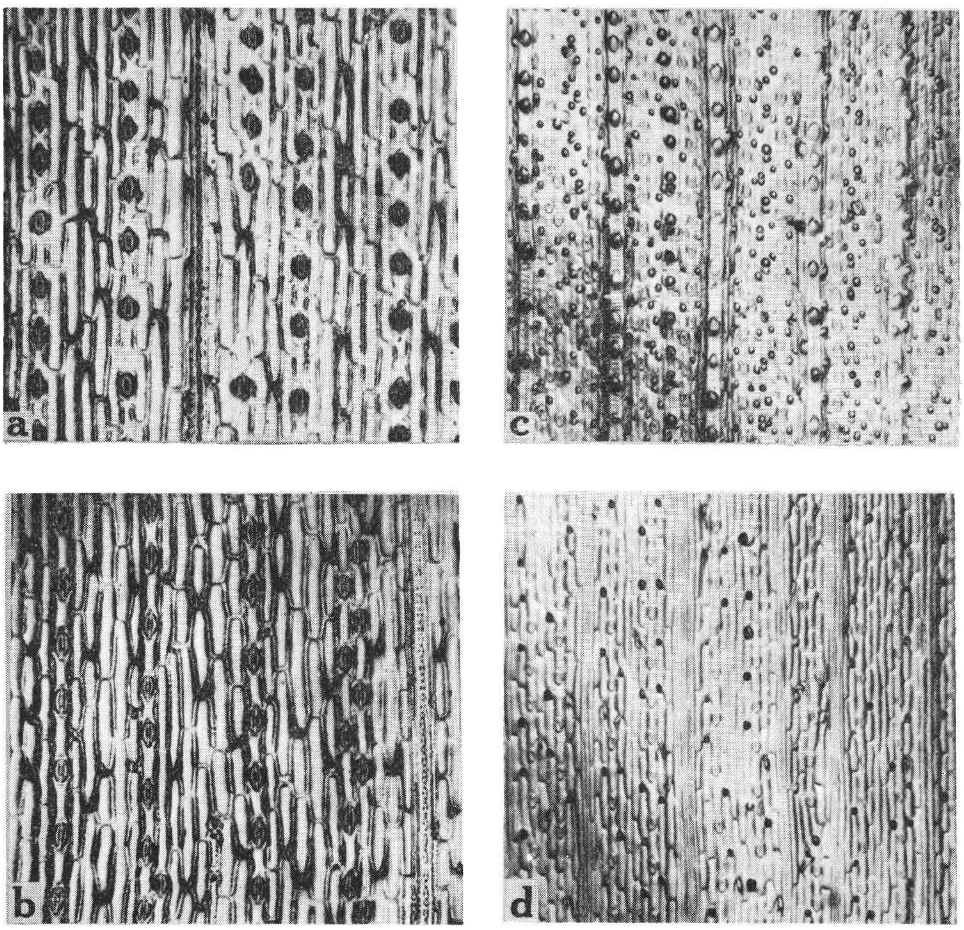


Figure 19. Sump patterns of under surface of leaves of *Setaria* species, a: *S. lutescens*, b: *S. pallide-fusca*, c: F_1 hybrid of *S. italica* (nonglutinous) × *S. viridis*, d: the second generation of *S. italica* treated with colchicine solution (0.25%) Magnification × ca. 80

vi) The second generation of *S. italica,* treated with colchicine solution, has stripes in various width at irregular distances like *S. italica*, but the spinules between veins are smaller than those of *S. italica*, and on veins extremely few (Figure 19).

vii) *S. chondrachne* has spinules mostly on veins and characteristic long spinules sporadically among the cells between veins. *S. excurrens* has spinules mostly on veins and sporadically between veins, which are arranged in regular and wide distances (Figure 20).

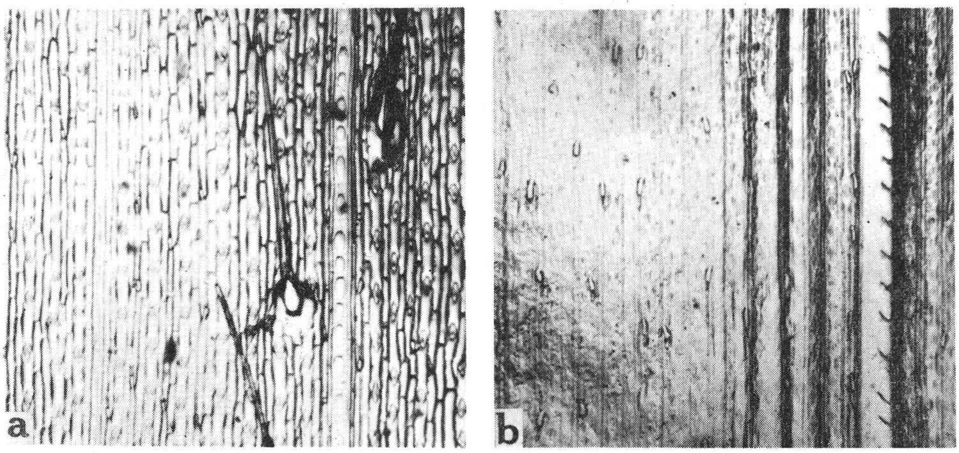


Figure 20. Sump patterns of under surface of leaves, of *Setaria* species, a: *S. chondrachne*, b: *S. excurrens* Magnification x ca. 80

Spodograms

The epidermal cells were classified into the following five kinds (Figure 21, 22): 1. elongated cell containing many crystals of ciliceous substances, 2. quartziferous cell, 3. spiniferous cell, 4. round cell, 5. small cell.

Spodograms of upper surface: i) the elongated cells which occupy the largest part of the epidermis, are rectangular in shape and arranged parallel to the rows of the veins. The side walls of the elongated cells are usually straight, but are wavy near the veins. ii) The quartziferous cell is rectangular or elliptical and mostly narrow in the middle part so that it looks like a pressed dumb-bell (Figure 21). These cells are arranged densely or apart forming a line or two along the veins. iii) The spiniferous cells are found along the veins or among the elongated cells between veins, often densely arranged like a chain of hooks. iv) The round cells are often irregularly polygonal in shape with straight cell walls. They are found mostly in the spe-

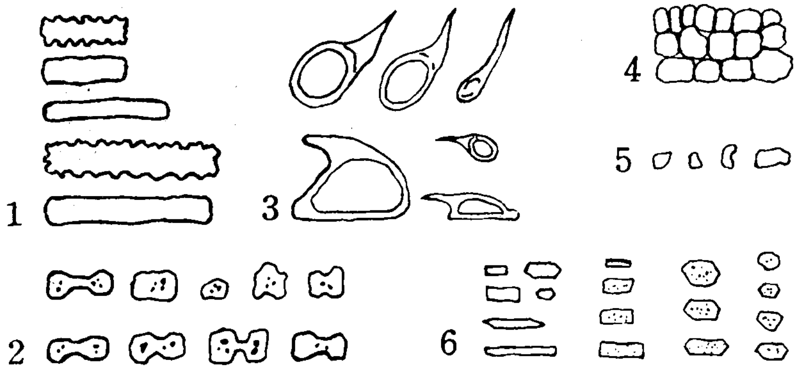


Figure 21. Epidermal cells in spodograms of *Setaria* species. 1. elongated cells, 2. quartziferous cells, 3. spiniferous cells, 4. round cells, 5. small cells, 6, siliceous substance

cies of group 2. v) The small cells are irregular in shape and found sometimes between elongated cells. vi) Stomata are very few, and no hairs were found.

Spodograms of the underside epidermis: the epidermal cells resemble those of the upperside both in arrangement and in shape. i) The elongated cells contain a large amount of siliceous substances, which are mostly square or hexagonal in shape. These cells along the veins are generally not very wavy. ii) The quartziferous cells of dumb-bell form are lined up under or among the spiniferous cells in one or two rows. Many rectangular quartziferous cells are also found next to both sides of rows of quartziferous cells in the dumb-bell form. iii) The spiniferous cells are less in the underside of leaves than in the upperside.

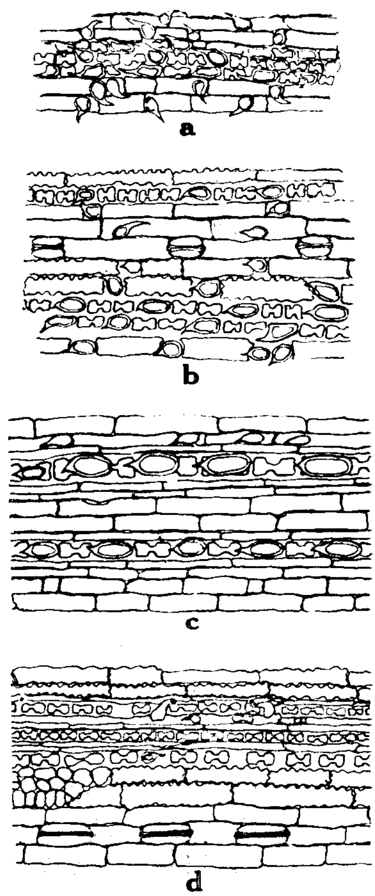


Figure 22. Spodograms of leaves of *S. italica* (a, b), and *S. lutescens* (c, d). a, c: epidermis of the upperside, b, d: epidermis of the underside Magnification ca. × 135

The characteristics in spodograms of *Setaria* are the dumb-bell shaped quartziferous cells and that the small cells are found very few. The cells of group 1 are the smallest and those of group 2 are the largest. Spiniferous cells are found generally more in number in the upperside of the leaves than in the underside.

7. Cytogenetical investigations - Cytological observations

The chromosome numbers in the genus *Setaria* were counted by AVDULOV (1931), as follows; *S. italica*: 2n=18 *S. viridis* var. *Weinmannia*: 2n=18 *S. plicata* 2n=36 (1928), *S. verticillata:* 2n=36 and *S. glauca:* 2n=36. In the Chromosome Atlas of Flowering Plants compiled by DARLINGTON and WYLIE (1955) there are also listed: *S. flabellata* (2n=18 by DE WETT 1954 b), *S. longispica* (2n=18 by MOFFETT et al. 1949), *S. intermedia* (2n=36 by KRISHNASWAMY et al. 1948), *S. magna* (2n=36 by BROWN 1948), *S. phragmitoides* (2n=36 by MOFFETT et al. 1949), *S. sphacelata* (2n=36, 2n=54 by MOFFETT et al. 1949), *S. chevalieri* (2n=54 by MOFFETT et al. 1949), *S. splendida* (2n=63 by MOFFETT et al. 1949), *S. macrostachya* (2n=72 by BROWN 1950), *S. palmifolia* 2n=54 by KRISHNASWAMY et al. (1954), *S. geniculata* (2n=72 by BROWN), *S. pallide-fusca* (*glauca*) (2n=18 by KRISHNASWAMY et al. 1954, 2n=36 by MOFFETT et al. 1949) and *S. glauca* (*lutescens*) (2n=36 by AVDULOV 1931), 2n=72 by BROWN 1948).

The author has established the chromosome numbers of the following species (Table 9); *S. viridis* BEAUV. 2n=18, *S. viridis* var. *pachystachys* 2n=18, *S. pycnocoma*

Table 9. *Setaria* species in the collection of the present author

Species	Chromosome number n	Chromosome number 2n	Japanese common name
Setaria italica (L.) P.B.	9	18	Awa
S. viridis Beauv.*	9	18	Enokorogusa
S. viridis Beauv. var. pachystachys Makino*	9	18	Hama-enokoro
S. pycnocoma (Steud.) Henr.* (*S. gigantea* Makino)	9	18	Oh-enokoro
S. Faberii Herrm.* (*S. autumnalis* Ohwi)	18	36	Aki-no-enokorogusa
S. verticillata (L.) P.B.	18	36	Zaratsuki-enokoro
S. chondrachne (Steud.) Honda*	18	36	Inu-awa
S. lutescens Hubbard (*S. glauca* (L.) P.B.) (*S. pumila* (poir.) Roem et Schult.)	18	36	Kin-enokoro
S. pallide-fusca (Schm.) Stapf*	36	72	Kotsubu-kin-enokoro
S. excurrens (Trin.) Mig.* (*S. plicata* (Lam.) T. Cooke)	36	72	Ko-sasakibi

* Chromosome numbers have been determined by the present author

2n=18, *S. Faberii* 2n=36, *S. chondrachne* 2n=36, *S. excurrens* 2n=72, and *S. pallide-fusca* 2n=72 (Figure 23, 24, 25).

S. Faberii which showed certain variations in plant colour, green or purple, had 36 chromosomes in the somatic cells and 18 pairs of chromosomes in PMC (Figure 23, 24).

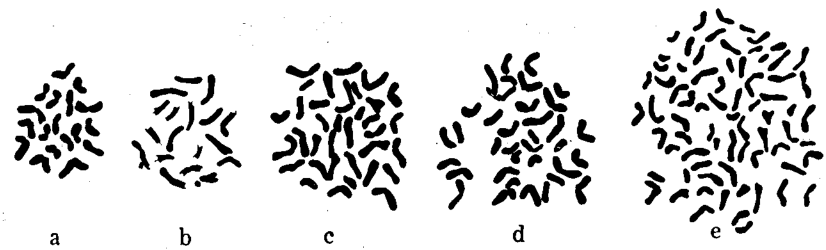


Figure 23. Somatic chromosomes in root tips of *Setaria* species, a: *S. italica* (2n=18), b: *S. viridis* (2n=18), c: *S. Faberii* (2n=36), d: *S. lutescens* (2n=36), e: *S. pallide-fusca* (2n=72) Magnification × ca. 2000

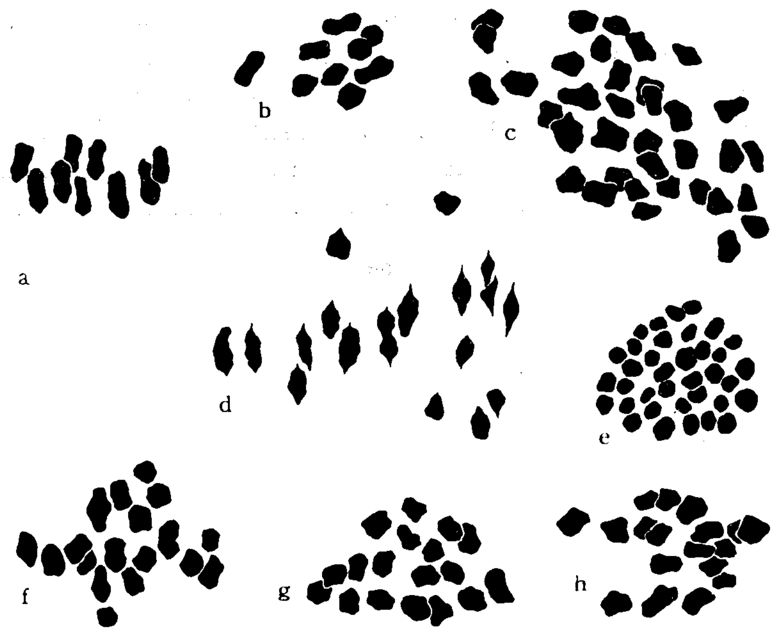


Figure 24. Meiotic chromosomes in PMC, a: *S. pycnocoma* (n=9), b: F_1 hybrid of *S. italica* (glutinous) × *S. viridis* (n=9), c: *S. pallide-fusca* (n=36), d: *S. chondrachne* (n=18), e: *S. excurrens* (n=36 f: *S. Faberii* (n=18), g: *S. verticillata* (n=18), h: *S. lutescens* (n=18) Magnification × ca. 2000

The chromosome number of *S. geniculata* was determined by the present author as 2n=72 in 1938. Recently, however, OHWI changed the species name as *S. pallide-fusca*. The chromosome number of *S. pallide-fusca* has been reported by KRISHNA-

SWAMY (1935) as 2n=18 and by MOFFETT et al. (1949) as 2n=36 after DARLINGTON & WYLIE (1955). But *S. pallide-fusca* in those reports is listed with the synonym of *S. glauca.* After several authors (AVDULOV and DARLINGTON & WYLIE) *S. glauca* is listed with the synonym of *S. lutescens* with the chromosome numbers 2n=36 or 2n=72. In consideration of the chromosome numbers, *S. pallide-fusca* by KRISHNASWAMY and by MOFFETT et al. seems to be *S. lutescens* or some other *Setaria* species.

In *S. pycnocoma*, five individuals of *italica* type, 14 of *viridis* type and eight of intermediate type were studied cytologically. All of them revealed 18 chromosomes without any abnormality in the root tip cells (Figure 24, 25). The progenies of these types showed a good chromosomal conjugation in PMC, though empty giant pollen (ca. 14%) were observed and pollen fertility was variable (2.30 - 91.00%).

Various intermediate types between *S. lutescens* and *S. pallide-fusca* were observed spontaneously but the chromosome number was counted in six individuals as n=36 and any univalent lagging outside the nuclear plate was not found. In three

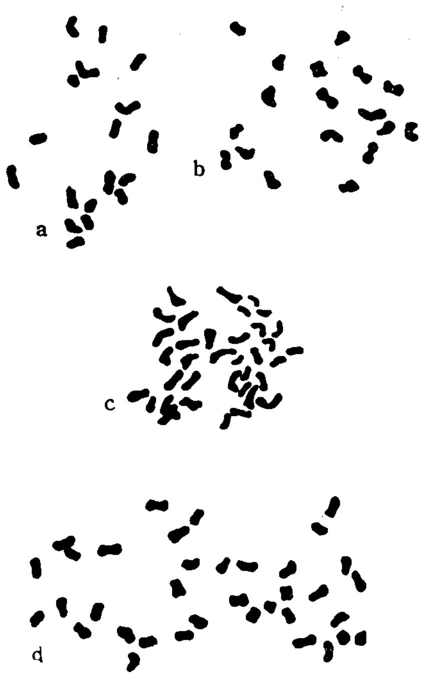


Figure 25. Somatic chromosomes in root tips of *Setaria* species, a: *S. viridis* var. *pachystachys* (2n=18), b: *S. pycnocoma* (2n=18), c: *S. chondrachne* (2n=36), d: *S. verticillata* (2n=36) × ca. 2000

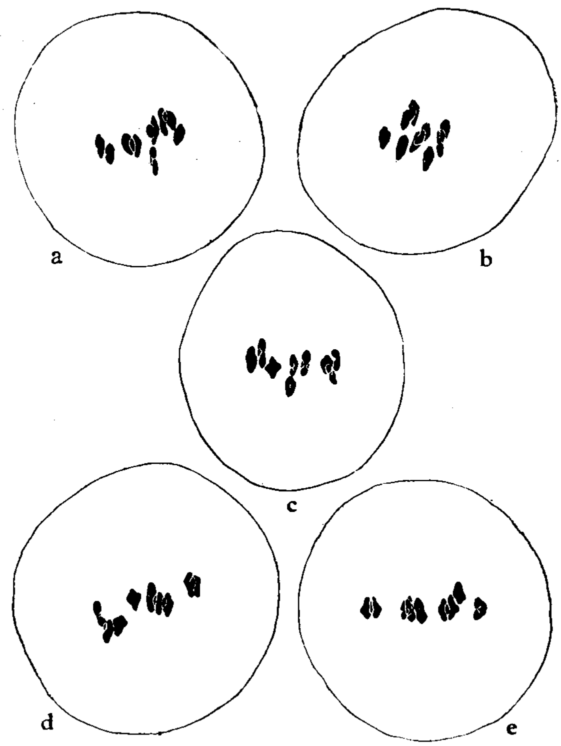


Figure 26. Meiotic chromosomes in PMC, a: *S. italica* (glutinous) × *S. italica* (nonglutinous), b: *S. viridis*, c-d: *S. italica* (glutinous) × *S. viridis*, e: *S. italica* (nonglutinous) × *S. viridis* Magnification × ca. 2000 (Kihara and Kishimoto 1942)

individuals 72 chromosomes were counted in somatic cells.

The F_1 hybrid of glutinous × nonglutinous in *S. italica* had normal chromosome pairing (9 pairs) without any irregularity (Figure 26). The tetrad formation appeared to be normal, and the pollen as well as seed fertilities were rather high (97.7 % and 89.00 % respectively) (Table 10, 11).

In an artificial F_1 hybrid between *S. viridis* (2x) and *S. italica* (2x), nine pairs of chromosome were seen. At the metaphase I of the meiosis the pairing of the chromosome was normal (Figure 26). The division proceeded normally and tetrads were formed normally. The pollen fertility was 85.00 % (Table 10). The frequency of sterile pollen grains (15%) is a little higher than that of the parents, which have approximately 5% of pollen sterility.

In F_1 hybrid between *S. Faberii* (4x) and *S. viridis* (2x), 2n=27 in somatic cells and 9II+9I in PMC were observed (Figure 27).

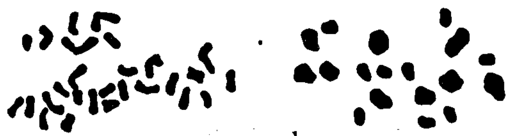


Figure 27. Chromosomes of F_1 hybrid of *S. Faberii* × *S. viridis*, a: somatic chromosomes 2n=27, b: meiotic chromosomes 9II+91 in PMC Magnification × ca. 2000

Table 10. Iodine potassium iodide reaction of pollen grains of *S. italica*, *S. viridis* and their hybrids

Plant	Iodine potassium iodide reaction				Pollen fertility %	
	Black	Intermediate	Reddish purple	Empty	Fertile	Sterile
M		0	219	13	94.9	5.6
U	226	0	0	12	95.0	5.0
v	217	0	0	12	94.6	5.4
U × M	70	3	113	0	98.4	1.6
U × M	70	3	86	2	96.9	3.1
M × v	72	12	123	23	84.8	15.2
M × v	96	15	153	3	93.3	6.7
M × v	60	19	110	12	84.5	15.5

M : glutinous *S. italica*, U : nonglutinous *S. italica*, v : *S. viridis*

Table 11. Seed fertility of *S. italica* (M,U), *S. viridis* (v) and their spontaneous hybrids

Plant	Fertile seeds	nferior seeds	% of fertile seeds
M	201	15	93.5
U	231	26	89.8
v	529	15	97.2
U × v	649	73	89.8
M × v	363	35	91.2
U × M	392	43	89.0

M : glutinous, U : nonglutinous

Genetic observations

In order to get informations for the techniques of artificial crosses, the flower construction was investigated (Figure 28). A floret consists of floral organs (one pistil with two plumose stigmas, three stamens and lodicules), palea (: inner glume, first glume or flowering glume) and lemma (: outer glume, second bract or flowering glume). A floret is formed in the axil of lemma on the rachilla. There are the first, second, and third empty glumes, which are sometimes called as the sterile glumes. The

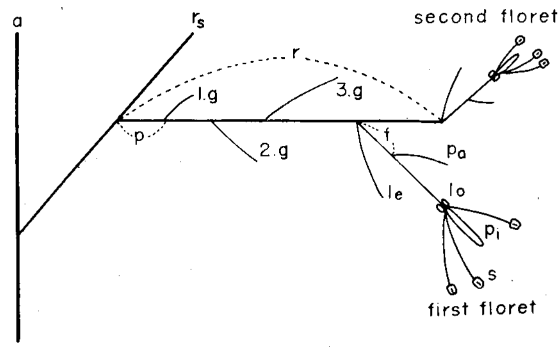


Figure 28. A diagram of a spikelet, a: main axis, rs: rachis, r: rachilla, p: pedicel, f: floral axis, 1.g: first empty glume, 2.g: second empty glume, 3.g: third empty glume, le: lemma, pa: palea, lo: lodicule, pi: pistil, s : stamen

lowest internode of rachilla is the pedicel. A spikelet consists of rachilla, one or two florets and three empty glumes (Figure 28). Spikelets are clustered on rachis diverged from a main axis of a panicle. In groups 1 and 2 the clusters are dense and the panicle looks spike-like, while in group 3 the clusters are loose or lax. As shown in Figure 12 and 13, florets of an apical cluster are modified into bristles in group 2. There are no awns in *Setaria*.

In group 1 the second floret is entirely degenerated. In group 2, however, the second floret has no pistil (degenerated) but three well developed anthers (Figure 29), pollen fertility being 72.33%. The second floret opens usually 3 - 7 days later than the first floret. To test whether the first floret is pollinated by the second floret, 20 first florets were emasculated and bagged together with not emasculated second florets and kept one month. An observation was made every day whether the stigma of the first florets remained fresh or whithered. It was thus found that the stigma of the first florets was not completely withered when the second florets flowered, indicating that there is a chance of pollination for the emasculated first floret by the pollen grains from the second floret. Therefore, the second floret must be also removed when the first florets are used for the crosses.

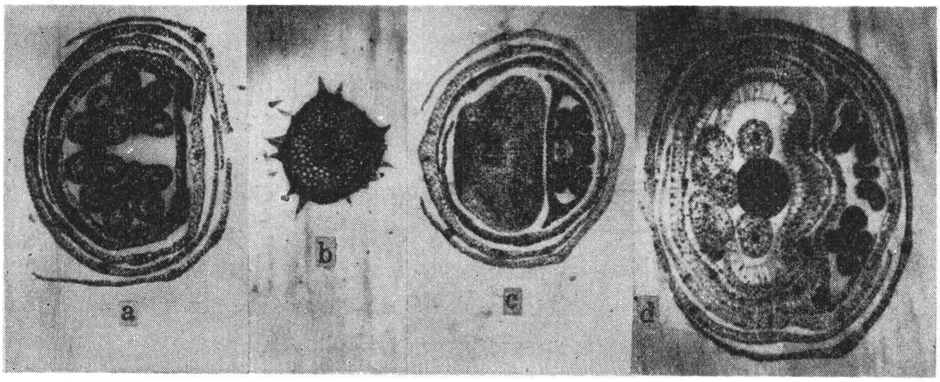


Figure 29. Cross sections of spikelets of *Setaria* species, a: *S. viridis* (group 1) having no second floret, b - d: *S. lutescens* (group 2), b: rachis having spinules, c: bottom of the first floret (left) and the second floret (right) with three anthers, d: the first floret (left) with three anthers and the second floret (right)

Before the crossing, the matured stigmas were pollinated with foreign pollen on hollow slide glass, which were then covered by a cover glass for the germination test of pollen grains. In 10 - 15 minutes all the pollen grains germinated very well and the pollen tubes grew into the tissue of stigma in any combinations among *S. italica* *S. viridis*, *S. Faberii*, *S. lutescens* and *S. pallide-fusca*.

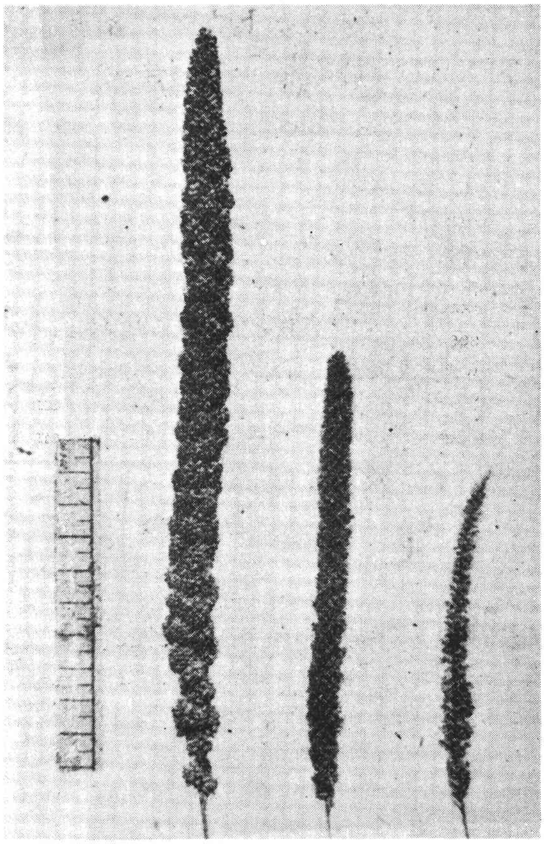
Crossing experiments were carried out between the varieties of *S. italica*. The cross fertilities were rather high as given in Table 8. The germination percentage of the hybrid seeds was 50 - 57%. i) *S. italica* BEAUV. var. *germanica* has smaller panicles in size than those of *S. italica maxima* and the F_1 hybrid had intermediate panicle size. ii) The endosperm of the seed from glutinous (♀) × nonglutinous (♂), showed a nonglutinous iodine reaction, indicating the xenia phenomenon. The F_1

hybrid expressed heterosis in the weight of a thousand seed grains in reciprocal crosses (2.2 - 2.4 g in the hybrid, 1.6 - 1.8 g in the parental plants) (Table 11). The nonglutinous character was dominant over the glutinous, and segregation in F_2 was 3 : 1 (Table 12).

Table 12. F_2 segregation of glutinous versus nonglutinous in respective crosses

Cross combination	Non-glutinous	Glutinous
U × M	152	48
M × U	125	33
M × v	184	53

U: nonglutinous *S. italica*, M: glutinous *S. italica*, v: *S. viridis*



a b c

Figure 30. Panicles of glutinous *S.* italica a), *S. viridis* (c) and an artificial F_1 (b). (Kihara & Kishimoto 1942)

The crosses between glutinous or nonglutinous *S. italica* (2x) and *S. viridis* (2x) gave the fertilities 51.3 - 84.13 % (Table 8). The germination percentage of the seeds obtained was 46 - 70 %. The F_1 plant resembled morphologically *S. viridis* in most respects (Table 13, Figure 4d, 30) having such characteristics as tillering, early owering time, long bristles, dark brown colour of anthers, seed shedding, and thin, small and dark brown seeds. The hybrid has more spikelets in number than *S. viridis* so that the panicles of the hybrid looked thicker and denser. When the hybrid plant was grown in a small pot, the plant showed very little difference from *S. viridis* in plant height and in panicle form. A well developed panicle of *S. italica* was about 25 cm long and bore about 1200 spikelets, each spikelet setting one seed. Average panicle length of *S. viridis* was about 4 - 8 cm and ca. 240 - 120 seeds were set per panicle, while a panicle of F_1 hybrid was about 10 cm long and set about 250 seeds. The seed fertility of F_1 hybrid was almost normal (ca. 90%) (Table 11). In F_1 hybrid of *S. viridis*

× glutinous *S. italica*, nonglutinous character of *S. viridis* was expected as a dominant character over glutinous. As shown in Table 12 the segregation of F_2 was 3 : 1 in reciprocal crosses.

Table 13. Morphological characteristics of *S. italica* (M : glutinous, U : non-glutinous), *S. viridis* (v - U) and their hybrid (U × v - U, M × v - U).

Character	M	U	v - U	U × v-U	M × v-U
tillering	few	few	many	many	many
time of flowering	late	late	early	early	early
bristle	short	short	long	long	long
colour of anther	white	brown	dark	dark	dark
pollen (glutinous or nonglutinous)	glutinous	nongl.	nongl.	nongl.	mixed
seed shedding	nonshed.	nonshed.	shed.	interm.	interm.
weight of 1000 grains	1.6 g	1.8	0.9	-	1.3
height of plant	120 - 130 cm		80 - 90	110 - 120	
length of panicle	20 - 30 cm		10	15	15

The cross, Montreal *S. viridis* × glutinous *S. italica*, was not successful. This was probably due to the difficulties of emasculation, since in Montreal *S. viridis* the floral parts do not open wide enough at the time of flowering and the anthers are entangled by the stigma. In the reciprocal cross, glutinous *S. italica* (♀) × Montreal *S. viridis* (♂), 18 seeds were obtained in 1960. They were sown in 1961, and 15 of them germinated. The mature F_1 plants were 5 - 10 cm in height and flowered at the same time as the Montreal *S. viridis*, i. e. May 25. The pollen grains were glutinous 4.96 : nonglutinous 4.61 : empty 90.43%.

From the crossing between *S. Faberii* and *S. viridis* not many seeds were obtained (Table 8). The cross fertility was higher in *S. Faberii* (4x)♀ × *S. viridis* (2x) ♂ (20.88 %) than in the reciprocal (14.48 %) (Table 8). The hybrid showed intermediate characteristics in the plant height and in seed size, being very low in seed fertility (ca. 2 %).

The cross fertility in *S. Faberii* (4x) ♀ × *S. italica* (2x) ♂ (26.92%) was higher than its reciprocal (15.70%). But the seeds did not germinate (Table 8).

The crosses between the species of groups 1 and 2 were tried in the combination of *S. Faberii* (4x) × *S. lutescens* (Mannheim) (4x) reciprocally but no seeds were obtained (Table 8).

The crosses between *S. lutescens* (4x) and *S. pallide-fusca* (8x) reciprocally gave very thin seeds and they did not germinate (Table 8).

8. Discussion

The number of *Setaria* species known in science is about 100 (Ohwi 1956). The species, chiefly domestic, in the author's collection were classified into three groups based on the morphological and physiological characteristics (Table 1, 2). The main differences between group 1 and group 2 are flowering season and the surface patterns of inner and outer glumes (Table 2, Figure 1, 10, 11). The species of group 1 flower in July and August, while those of group 2 flower in September and October. The surface of inner and outer glumes in the species of group 1 is smooth, while the species of group 2 have a transversely rugose surface of inner and outer glumes. The species of groups 1 and 2 have spike-like panicles.

The species of group 3 differ from above two groups, in having a panicula inflorescence. In group 3 *S. chondrachne* has a smooth surface of inner and outer glumes like those of group 1 (Figure 15). The other two species, *S. palmifolia* and *S. excurrens*, have inner and outer glumes with transversely rugose surface.

The chromosome numbers of following six species were determined by the present author, i. e. *S. viridis* var. *pachystachys* 2n=18, *S. pycnocoma* 2n=18, *S. Faberii* 2n=36, *S. excurrens* 2n=72, *S. chondrachne* 2n=36, and *S. pallide-fusca* 2n=72.

In Darlington's "Chromosome Atlas" (1955), the chromosome number of *S. chondrachne* is given as 2n=38 by Ono et al. (1953). This is probably a miscitation, because, according to Ono's personal correspondence, he has never studied on the chromosome number of genus *Setaria*. The present author has found 2n=36 in the somatic cells of this species.

The chromosome number of *S. geniculata* was determined by the present author as 2n=72 in 1938. However, it has become clear that this species is not *S. geniculata*, but *S. pallide-fusca* for the following reasons. *S. geniculata* and *S. pallide-fusca* resemble morphologically closely, but *S. geniculata* has rhizome and is perennial, while, *S. pallide-fusca* has no rhizome and is annual (Hitchcock 1951, Hubbard & Vaughan 1940, Bor 1960 and Jansen 1953). Since *S. geniculata*, investigated by the present author in 1938, has no rhizome and is annual, this species is *S. pallide-fusca*.

In the list of chromosome number of Darlington & Wylie (1955) the chromosome number of *S. pallide-fusca* is given as 2n=18 by Krishnaswamy (1955) and as 2n=36 by Moffett et al. (1949). On the other hand *S. glauca* is listed by a synonym *S. lutescens*. The chromosome number of *S. glauca* was 36 (2n) by Avdulov (1931) and 72 (2n) by Brown (1948). The plant with 2n=36 seems to be *S. lutescens* and the other with 2n=72 seems to be *S. pallide-fusca*, and the plant with 2n=18 may be another species.

By the experiment of the germination of pollen grains on the foreign stigma as mentioned before, it was found that the pollen grains germinated in all the combinations of species of *Setaria* and pollen tubes grew well into the tissue of the stigma. But in nature there might be certain factors which control natural crosses; for instance the difference in plant height will hinder the natural pollination in some extent in *S. Faberii* (4x) ♀ × *S. viridis* (2x) ♂ and the difference of the flowering seasons will result the physiological isolation between the species of groups 1 and 2. The natural obstacle against the crossing is also the low cross fertility and low seed fertility. Although there will be the crossing chances in *S. viridis* (♀) × *S. Faberii* (♂) or *S. lutescens* × *S. pallide-fusca* (reciprocally), the artificial cross fertility was very low, and the hybrid seeds did not germinate.

It is noteworthy that the F_1 hybrid of glutinous × nonglutinous in *Setaria* expressed heterosis regarding the weight of a thousand seed grains of the hybrid, namely 2.2 - 2.4 g in reciprocal crosses, while that of the parental plants was 1.6 - 1.8 g (Table 13).

In the natural condition the crossing, *S. viridis* (♀) × *S. italica* (♂), would occur in this direction more frequently than in the reverse, because *S. italica* is taller than *S. viridis* and the pollen grains of the former fall down onto the latter. *S. pycnocoma* is found very often in the fields of *S. italica* and is supposed to be the hybrid of the two species. As shown in Figure 4, panicles of *S. pycnocoma* resemble extremely F_1 hybrid of *S. italica* × *S. viridis*. But in great majority *S. pycnocoma* is larger than the F_1 hybrid in plant height, leaf width and panicle length. They have been classified morphologically into three types (Table 5); (1) *italica* type, (2) *viridis* type and (3) intermediate type. Although the seed fertility was low (73.40, 6.78, 40.83% respectively), all the types had $2n=18$ and $n=9$ (9II in meiosis) (Figure 24, 25) and no chromosomal abnormality was observed either in somatic cells or in PMC.

In the field of cultivation of *S. italica*, as the *italica* type is not easily distinguished from *S. italica*, it is harvested together with *S. italica*, while the seeds of intermediate type and *viridis* type shed easily at maturation resulting inevitable weed for generations.

The normal conjugation of chromosomes in meiosis in the artificial F_1 hybrid of *S. italica* × *S. viridis* indicated that these two species have a homologous genome (A) in common. In the F_1 hybrid of *S. Faberii* (4x) ♀ × *S. viridis* (2x) ♂ 9II+9I chromosomes were observed in the meiotic metaphase. Therefore it can be concluded that *S. Faberii* has a genome homologous with the genome of *S. italica* or *S. viridis*, namely (A) and nonhomologous genome (B). Accordingly, the genome constitution of *S. Faberii* could be given as AABB.

S. viridis has been thought to be the ancestor of *S. italica* (KOERNICKE 1955 WERTH 1937, LI et al. 1942, 1944 and HEGI 1906). The wild species, such as *S. viridis* and *S. Faberii*, are widely distributed in Eastern Asia, Northern Africa, North America, Siberia, Southern Europe, and also in the south east part of Finland. After HEGI (1906) *S. viridis* var. *major* which is the intermediate form between *S. italica* and *S. viridis* grows everywhere. Accordingly, HEGI proposed an evolutional process as: *S. viridis* → *S. viridis* var. *major* → *S. italica* var. *germanica* → *S. italica* var. *maxima*.

This suggestion by HEGI is not acceptable for the following reasons. Hegi's *S. viridis* var. *major* in the picture (1906) appears to correspond to *S. Faberii*, which morphologically has the intermediate feature between *S. viridis* and *S. italica* in size and form of plant, of panicle and of seed. *S. Faberii* is tetraploid (KISHIMOTO 1938), while other species in the Hegi's evolutional process are all diploid.

S. viridis always occur wherever *S. italica* is cultivated. These two species have equally $2n=18$, and cross rather easily with each other. The cross fertility rates are 67.73% in *S. italica* (♀) × *S. viridis* (♂) and 56.01% in the reciprocal, respectively. The germination ratio of hybrid seeds was 46 - 70%. In meiosis of the artificial F_1 hybrid the chromosomes conjugate normally forming 9II at metaphase, and no univalent is observed. There is no significant difference in chromosomal conjugation between F_1 hybrid and *S. italica* or *S. viridis*. The seed fertility of F_1 was ca. 90%. The characteristic feature of wild *S. viridis*, such as plant tillering, seed shedding, dark colour of seed and anther, and nonglutinous endosperm, were expressed in F_1 plant as dominant over the characters of *S. italica*. Nonglutinous versus glutinous segregated in F_2 with Mendelian segregation of 3 : 1 (KIHARA & KISHIMOTO 1942). Nonshedding character, which is the very important characteristic of cultivated plants, may have been discovered firstly in the course of evolution. Through many generations ever since the present *S. italica* has developed by continuous selection.

In conclusion, the origin of cultivation of Italian millet will be considered. The cultivation of *Setaria italica*, is widely spread in Eastern Asia (North China, Manchuria, Korea, Okinawa, Formosa, Japan and India), Middle East (Caucasus), Asia Minor, Russia, Middle and Southern Europe and U. S. A.. The northern limit of its cultivation is lat. 50° N. in Europe and ca. 45° N. in U. S. A., and it is grown along the isothermal line of 17° - 20° C in June and July in Europe (WERTH 1933).

In Japan, it is cultivated in Tohoku (Aomori and Iwate Prefectures), Kyushu (Kumamoto, Kagoshima and Nagasaki Prefectures) and also in the mountainous districts of Nagano, Ibaraki and Hiroshima Prefectures. In some districts of Kagoshima Prefecture, where the rainfall is very scarce, *Setaria italica* and sweet potatoes were staple food until the farmers had to take their allotments of rationed rice (1943). But still today they keep to their habit of eating *Setaria italica* mixed with rice.

In China it was one of the five important cereals planted by Shennung 神農, 2700 B.C. (Ssumachien 司馬遷 163 - 84 B.C.), which included rice, wheat, sorghum, soybean and foxtail millet.

In Ukraine and Hungary, Mohar, a variety of *S. italica,* is an important forage crop. In Persia *S. italica* was already cultivated in olden times (HOOPS 1905).

In Europe the remains of the millet are found in all the periods from the end of the Stone Age, through the Bronze Age, up to the Iron Age. Poland, Hungary, Rumania, Bulgaria, Yugoslavia, Czechoslovakia, U.S.S.R., Germany, France and Northern Italy are the main countries of millet cultivation. Since *S. italica* is not found in the remains of the middle Stone Age, it can not belong to the very old cereals (BECKER-DILLINGEN 1927). In England it seems not to have been cultivated (PERCIVAL 1932).

The millet cultivation extended in Europe across the Alps toward the south as far as South Italy and Balkan Peninsula. In Crete it was found by excavation (WERTH 1937). But the cultivation is localized rather in the north, it did not spread across the Mediterranean Sea to the south in the neolithic Age. *S. italica* has never been important food in the Mediterranean regions.

In ancient Egypt it was not planted, and its practical cultivation has not developed there (HOOPS 1905). Also in Canary Islands the natives are still living in the primitive way of Neolithic Age, and there everything can be found of that age except *S. italica* (MEYER 1896). *S. italica* does not seem to be important as a food in the North West of Africa.

It is said, that the native land of *S. italica* is somewhere in the northern part of India (KOERNICKE 1855), India (WERTH 1937) or in the south eastern part of Europe, Egypt and Africa (BECKER-DILLINGEN 1927). After BECKER-DILLINGEN, *S. italica* had been the main food of the ancients before the rise of the Indo-Germans.

The native land of *S. italica* should be the regions bordering the north frontier of India and Northern India. The cultivation of *S. italica* spread into East Asia conforming with the current of culture toward north east, and into Europe toward north west through the regions both sides of the Black Sea. In another direction from India to Africa the cultivation should have accompanied the livestock farming into Ethiopia and further to the South West of Africa. The center of most varieties of *S. italica* is in Middle and East Asia (Manchuria, Mongolia, China and Japan), but extends as far west as Afghanistan and Iran (SCHIEMANN 1932, VAVILOV 1931). In these regions the Asiatic people lived under seminomadic conditions. Europe can not be considered as the native land where they originated, because only a limited number of varieties is found. Probably the cultivation has spread towards Europe also from East Asia secondarily.

9. Summary

1) Chromosome numbers of six species of *Setaria* were established by the present author (Table 9).

2) The *Setaria* species of the author's collection have been classified into three groups morphologically and physiologically (Table 1, 2).

3) The germination percentage of seeds of *S. italica, S. viridis, S. Faberii, S. lutescens* and *S. pallide-fusca* fell remarkably in two years after harvest, and in five years the seeds lost their power of germination. The seeds of *S. italica, S. chondrachne* and the *italica* type of *S. pycnocoma* require no dormancy period, while other species require a dormancy period of four-six months.

4) The populations of groups 1 and 2 are isolated, because the flowering season of the former is July - August and that of the latter September - October.

5) The epidermal cells in the leaf of *Setaria* were observed by Sump method and in spodogram preparations (Figure 18 - 22). Dumb-bell shaped quartziferous cells are remarkable and the number of small cells is very small.

6) The artificial crosses were made among five species of *Setaria* (Table 8).

i) the varietal crosses of *S. italica* and the crosses of *S. italica* (2x) × *S. viridis* (2x) showed a high crossability and all of F_1 hybrids had the normal meiosis forming nine bivalents in PMC. *S. pycnocoma*, supposed to be a natural hybrid of *S. italica* × *S. viridis*, formed also normal nine bivalents in PMC.

ii) The crosses of *S. lutescens* (4x) × *S. pallide-fusca* (8x) set poor seeds which did not germinate.

iii) The crosses of *S. Faberii* (4x, group 1) × *S. lutescens* (4x, group 2) was unsuccessful.

iv) In Fl hybrid in the cross of *S. Faberii* (♀) (4x) × *S. viridis* (♂) (2x) 27 chromosomes in somatic cells and 9II+9I at the first meiotic metaphase in PMC were observed.

v) *S. italica* and *S. viridis* have the homologous genome and *S. Faberii* has a different genome which is not homologous with that of *S. italica* or *S. viridis*.

7) The native land of *S. italica* should be in the regions bordering the north frontier of India and Northern India.

8) It is proved that *S. viridis* is closely related to *S. italica*, based on the following reasons: i) both of them have the same chromosome number (2n=18), ii) *S. viridis* occurs wherever *S. italica* is cultivated, iii) the two species have many morphological, physiological and cytological characters in common, iv) the two species can be crossed easily and their F_1 has high seed fertility, v) F_2 shows a Mendelian inheritance in endosperm characters.

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